

REPRODUCTIVE ENERGETICS OF BLUE-EYED SHAGS IN ANTARCTICA

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Time and energy budget estimates have been used to measure parental investment of birds despite the difficulties of comparing the consequences of proximate energy allocation on future reproductive success (Walsberg 1983). These estimates are popular, in part, because they encompass the risks, costs, and benefits of parental investment simultaneously, all of which must be balanced if parents are to achieve maximum lifetime fitness (Trivers 1974, Patterson et al. 1980, Wittenberger 1982).

Measuring energy expenditure in the field is usually accomplished by converting the bird's behavior and thermal relation to the environment to energy expended. Although these techniques have been criticized for their inaccuracy (Weathers and Nagy 1980, Williams and Nagy 1984), with adequate sampling, most error in energy estimates results from the use of somewhat arbitrary conversion factors expressed in multiples of standard metabolic rates. Ettinger and King (1980) have demonstrated that inaccuracies in estimating individual components of a time budget resulted in little variation of daily energy expenditure if no large errors were made in estimation of energetically costly activities or activities that consumed large amounts of time (see also Mugaas and King 1981). Even so, by using the same conversion factors for all individuals, individual comparisons should be valid even if they do not represent accurate energy expenditures.

We here report time and energy budget estimates of individual Blue-eyed Shags (*Phalacrocorax atriceps bransfieldensis*) in Antarctica. We asked two questions: (1) What are the patterns of time and energy allocation between sexes, and (2) does each sex of these monogamous birds equally allocate time and energy into reproduction?

METHODS

The study area and methods are partially described in Bernstein and Maxson (1984). For coherency, parts of the methods from that publication are repeated.

We collected 3198 bird-h of time budget data from 15 January 1979 to 1 April 1979 and from 23 September 1979 to 15 March 1980 at a colony of Blue-eyed Shags on Shag Island, 5 km southwest of Palmer Station, Anvers Island, Antarctica (64°46'S, 64°03'W). There were 485 nests on 31 December 1978, and 326 on 19 December 1979. During sample days, we observed 2-10 nests simultaneously every 30 sec, at the tone of a metronome (see Wiens et al. 1970), either from dawn to dusk or for 24 h during periods of continuous daylight. All statistical calculations were based upon these nests, which were observed for continuous

TABLE 1
AVERAGE MONTHLY WEATHER DATA AT PALMER STATION

Month/year	Temperature (°C)	Percent cloud cover	Wind speed (knots)
Jan 1979	1.85 ± 0.20 ^a	82.9 ± 3.14	6.73 ± 0.81
Feb 1979	1.35 ± 0.24	91.8 ± 2.20	9.98 ± 1.06
Mar 1979	0.73 ± 0.16	94.5 ± 1.37	8.31 ± 0.78
Sep 1979	-4.96 ± 0.53	89.3 ± 2.37	12.13 ± 1.29
Oct 1979	-3.58 ± 0.36	93.9 ± 2.00	11.34 ± 1.16
Nov 1979	-0.44 ± 0.31	90.0 ± 2.34	6.22 ± 0.65
Dec 1979	1.65 ± 0.19	83.7 ± 3.14	4.88 ± 0.60
Jan 1980	1.86 ± 0.17	78.7 ± 3.11	5.03 ± 0.56
Feb 1980	2.52 ± 0.17	85.0 ± 2.89	5.95 ± 0.68

^a Mean ± SE.

lengths of time (see Table 2 for sample sizes), but time budget graphs reflect all nests observed. In addition, 84 bird-h, 64 of which were filmed at one nest for 32 continuous h, were obtained using a Super-8 movie camera timed to expose one frame approximately every 30 sec. No observations were conducted during heavy rain or during winds greater than 30 knots. These conditions were infrequent (Table 1). Blinds, 10–25 m from the birds, concealed us after September 1979, but the shags seemed undisturbed unless we were close to their nests. Shags were captured with short-handled nets, examined for molt, weighed with a 5 kg Pesola spring scale, and banded with stainless steel bands. Birds under observation were color banded. Adult shags were sexed by body and bill size and by vocalizations (Bernstein and Maxson 1984, Shaw 1984).

Behavioral activities included preening, resting, standing, flying, walking, nest building, incubation, brooding, courtship, pairbond maintenance, copulation, chick feeding, chick preening, face-offs, gathering nest material (algae) nearby (Bernstein and Maxson 1982a), foraging, swimming above water, diving (and swimming underwater), and bathing. Shags were assumed to be foraging when absent from the nest or from the vicinity of the colony.

Blue-eyed Shags maintained rigid, sexually distinct, activity patterns throughout the colony except during periods of severe weather or extensive ice cover (Bernstein and Maxson 1984). The only other disruptive factor was prey piracy by South Polar Skuas (*Catharacta macormicki*) early in the breeding season (Maxson and Bernstein 1982). Therefore, time budget data collected on the observed pairs probably applied to most of the colony.

Data were grouped by sex for each of the following stages of the breeding cycle: prelaying, laying-incubation, brooding, and fledging periods. Criteria used to determine these stages are described in Bernstein and Maxson (1984).

Pack ice limited travel to the island during early stages of the breeding cycle and the early and middle chick rearing periods, and data for these brood periods are few.

To determine climatic variables affecting energetics of thermoregulation by gular fluttering (a thermoregulatory behavior), we observed 10 nests during one 24-h period. Every 15 min, we recorded the proportion of shags gular fluttering, wind speed with a hand-held anemometer, relative humidity with a sling psychrometer, air temperature at nest level with a thermistor, and relative brightness with a light meter in a single lens reflex camera. Daily weather data were also collected at 08:00, 14:30, and 20:00 at Palmer Station.

Calculation of Daily Energy Expenditure.—Daily Energy Expenditure (DEE) was calcu-

lated as multiples of standard metabolic rates (SMR). Ricklefs and Matthew (1983) measured oxygen consumption for six Blue-eyed Shags and found that SMR was about twice that predicted by Lasiewski and Dawson's (1967) equation. This resulted in a SMR of 60.13 kJ/h for males and 53.57 kJ/h for females.

The following conversion factors were used: night and daytime resting ($1.2 \times \text{SMR}$) (King 1974), standing ($1.25 \times \text{SMR}$) (Aschoff and Pohl 1970), preening and preening chicks ($2.5 \times \text{SMR}$) (Custer and Pitelka 1972), incubating ($1.25 \times \text{SMR}$) (King 1973, Walsberg and King 1978), brooding Early chicks ($1.25 \times \text{SMR}$) (this study), brooding Middle chicks ($1.2 \times \text{SMR}$) (this study), nest building, walking, feeding chicks, and face-offs ($3.0 \times \text{SMR}$) (Orians 1961, King 1974), pairbond maintenance ($3.0 \times \text{SMR}$), courtship ($3.5 \times \text{SMR}$ for males, $3.0 \times \text{SMR}$ for females) (Orians 1961 and this study), foraging ($1.8 \times \text{SMR}$) (see below), bathing ($10 \times \text{SMR}$) (this study), flying ($15.2 \times \text{SMR}$) (King 1974), and gathering nest material ($5.9 \times \text{SMR}$) (see below). The DEE was calculated for each bird and averaged to obtain a mean DEE for each sex during each breeding period.

Feather replacement costs energy (King 1974, Dunn 1979, Mugaas and King 1981, Walsberg 1983). Molt, however, was not frequent during the breeding season (Bernstein and Maxson 1981), and was not included in estimation of DEE.

Energy cost of foraging involved the following: flight speed, distance traveled, and behavior while away from the nest. Blue-eyed Shags took $1.15 \text{ min} \pm 0.08 \text{ [SD]}$ ($N = 13$) to travel 1 km during normal flight in winds under 10 kmh, and, therefore, flew at approximately 52 kmh. It was not possible to follow shags on foraging flights, but judging from the direction taken on most days, knowledge of ice-free habitats, and location of other shag colonies, a conservative estimate of 10 km was made for average distance traveled to forage, and a 20-km flight was added to the daily time budget. For comparison, DEE was also calculated with a 30-km and 40-km roundtrip. Because shags usually foraged beyond permissible travel boundaries around the station, our time budget data on foraging behavior only totaled 11.5 h over 5 days on 1-4 birds at a time. Larger foraging flocks were observed early in the breeding season, but no time budget data were collected on these birds.

The costs of swimming and diving were estimated from other studies. Although Kanwisher et al. (1981) reported an immediate 50% tachycardia and an increase in breathing rate as Double-crested Cormorants (*P. auritus*) surfaced after diving, no difference was noted in the heart rate of shags between normal above water swimming and diving. Therefore, swimming and diving were given the same energy conversion values based on Prange and Schmidt-Nielsen's (1970) estimate of above water swimming in the Mallard (*Anas platyrhynchos*). Because time spent in increased oxygen consumption during the interdiver occurred for only an extremely small proportion of the day, it was not accounted for in the energy budget.

Energetic costs of gathering nest material, which involved males only, encompassed several separate behavioral patterns (Bernstein and Maxson 1982a, 1984). Males flew to nearby shallow water and collected benthic algae during short dives. Distance to the algae beds was approximately 0.4 km, and the flight time for a round trip was 0.9 min. Average time for a complete trip was $4.4 \text{ min} \pm 1.8$ ($N = 47$) with time used in diving making up the difference between total trip time and round-trip flight time. When appropriate conversion factors are applied, energy cost of gathering nest material was $5.9 \times \text{SMR}$. Shaw (pers. comm.) has noted females also gathering nest material, but we did not.

The cost of egg production must be added to the energy budget of females during prelaying and laying-incubation periods. Additional data to make this calculation were collected by Shaw (1981, 1984), who had access to a large, banded colony of Blue-eyed Shags.

Three-egg clutches were most common (2.5 ± 0.6 , $N = 811$ nests, this study; 2.31-2.84,

$N = 1230$ from 1979–1981, Shaw, in press). Freshly laid eggs were weighed in the field with a 100-g Pesola spring scale. Average egg weight was $59.1 \text{ g} \pm 3.99$ ($N = 13$) for this study; and Shaw (1981), who was able to measure more smaller, third eggs in the clutch, found a mean weight of 54.6 g ($N = 623$). The combined average egg weight from the two studies was 54.7 g , and this value was used to calculate costs of egg production because it allowed for smaller, third eggs. Shaw (1981) measured the egg-laying interval at 2.59 days ($N = 544$) for 3-egg clutches, which was the value used in calculations. Two-egg clutches had a longer laying interval (Shaw 1985).

Two freshly laid first eggs were collected and analyzed in an adiabatic oxygen bomb calorimeter. The eggs were oven dried at about 15.5°C and ground to a uniform consistency with a mortar and pestle. The ground egg shell was added before analysis. Ten samples from each egg were tested.

Egg samples averaged $3.85 \text{ kJ/g} \pm 0.40$ dry weight or approximately 220 kJ/egg . Assuming a 70% efficiency of production (King 1973), each egg costs about 313 kJ to produce. If approximately 7 days are required for egg production, given the egg-laying interval (above), maximum energy expenditure for a clutch of 3 eggs equals 134 kJ/day during prelay and 139 kJ/day during laying-incubation (see King 1973).

Maximum energy costs of testicular and ovarian development are small (Walsberg 1983). Distributed over an uncertain number of days, energy costs of gonadal growth were assumed to be minimal and were not included in the DEE.

RESULTS

Meteorological data collected in conjunction with gular-flutter patterns revealed no definite trends. Shags tended to gular flutter at temperatures above 2°C and when exposed to bright sun, but some also gular fluttered in misty conditions near 0°C . The only predictable time of gular flutter was at return to the nest from a foraging flight, when the shags were overheated from exertion. Meteorological data collected at Palmer Station indicated that temperature, wind speed, and cloud cover varied little within a month and were similar among months of the breeding season, especially December through March when chicks were present (Table 1).

Observations of shags away from the colony indicated that only 8.4% of the time was spent swimming or diving, and 91.6% of the time was spent preening, standing, or resting on shore. Short flight times between shore and water and vice versa were not accounted for in the estimation of DEE.

Fifteen observations were made of foraging shags for 40 sec–50 min. Dive and interdive times were recorded for either single birds or flocks of up to 84 individuals, which dove synchronously. Dive times ranged from 5 sec to 3.5 min, and interdive times were between 2 sec and 4.3 min. Flocks of over 200 foraging shags were observed in December, and they also remained submerged for up to 3.5 min. It is not known if this foraging tactic was used throughout the breeding season. Lone shags remained submerged for less time than did the majority of shags in a group

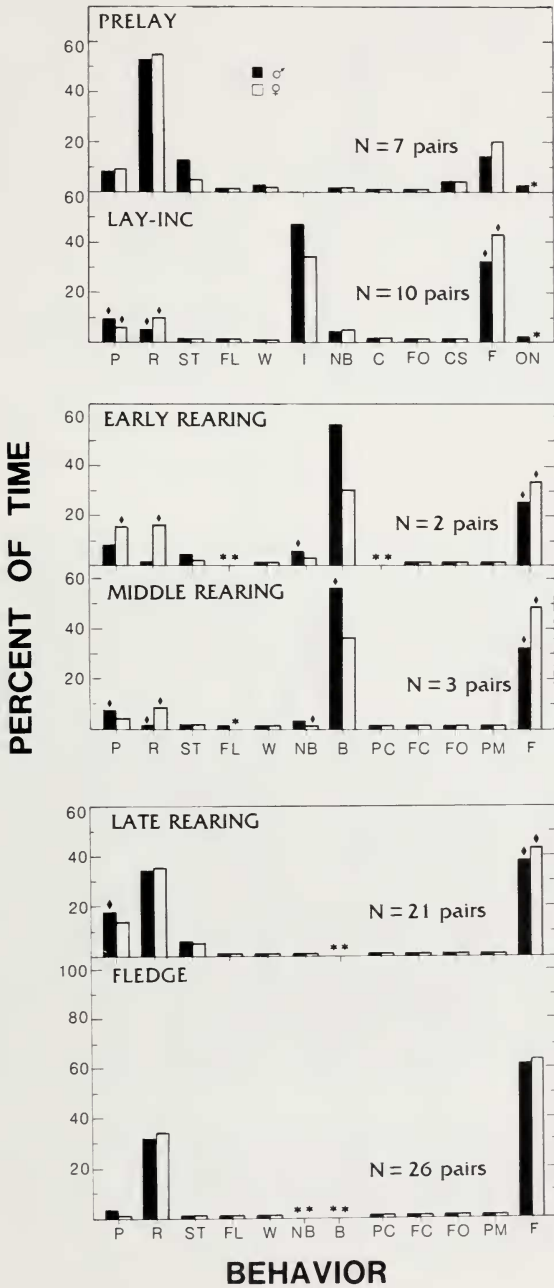
(94 sec \pm 50.5 [N = 35] and 189.62 sec \pm 22.5 [N = 13]; $t = 6.55$, $df = 46$, $P < 0.001$). Only 4 dives of lone shags exceeded the minimum dive length of 150 sec by groups of shags.

Time budgets.—Most patterns of behavior illustrated in Figs. 1 and 2 are described in Bernstein and Maxson (1982a), and not all of them will be discussed in this paper. A minimum of 9 h of darkness prevented shag activity away from the nest during the prelaying period, and detailed behavioral observations were not possible during this time. Colony checks at night, however, revealed that most nests had pairs present. Therefore, preening, resting, and sitting (pooled together into "Present at the nest" in Fig. 2) comprised over 70% of the 24-h day (Figs. 1, 2). Foraging time could be reduced because shags were not feeding chicks and only had to forage for themselves. Males had to establish a territory and defend the nest site until successfully paired, and after pairing, both sexes had to build and defend a nest against territory usurpers and nest-material thieves (Bernstein and Maxson 1982a). No extra-pair copulation attempts were observed, and mate defense did not appear to be a factor in time allocation. Time spent in courtship, however, indicated the greatest time commitment to pairbond maintenance from prelaying to fledging (Figs. 1, 2).

Males incubated more than females, which spent more time foraging (Figs. 1, 2). Once laying began, nest building activities increased for both sexes, but females spent more time in actual manipulation of nest material, which males continued to gather nearby. During the laying-incubation period, neither sex spent much time at the nest when not incubating, but after the chicks hatched, there was a decrease in foraging for both sexes (Figs. 1, 2). This resulted in an increase in female presence at the nest that was not seen in males because the latter brooded more than females while females rested by the nest (Figs. 1, 2).

Females gradually spent less nonbrooding time at the nest as the breeding season progressed (Figs. 1, 2). Instead of engaging in behavior centered at the nest, females disproportionately increased their foraging time com-

FIG. 1. Time Budgets for Breeding Season. P = Preen, R = Rest, ST = Stand, FI = Fly, W = Walk, I = Incubate, B = Brood, PC = Preen Chicks, FC = Feed Chicks, NB = Nest Build, C = Copulate, CS = Courtship, F = Forage, FO = Face-off, PM = Pair-bond Maintenance, ON = Gather Nest Material, * = No time spent in this behavior. Diamonds above the bars indicate standard errors between 0.5 and 2.5%; no diamonds above the bars indicate standard errors less than 0.5%. Darkness prohibited observations between 20:00 and 06:00 during prelaying and between 24:00 and 04:00 during the fledging period. Shags were resting at the nest during these times.



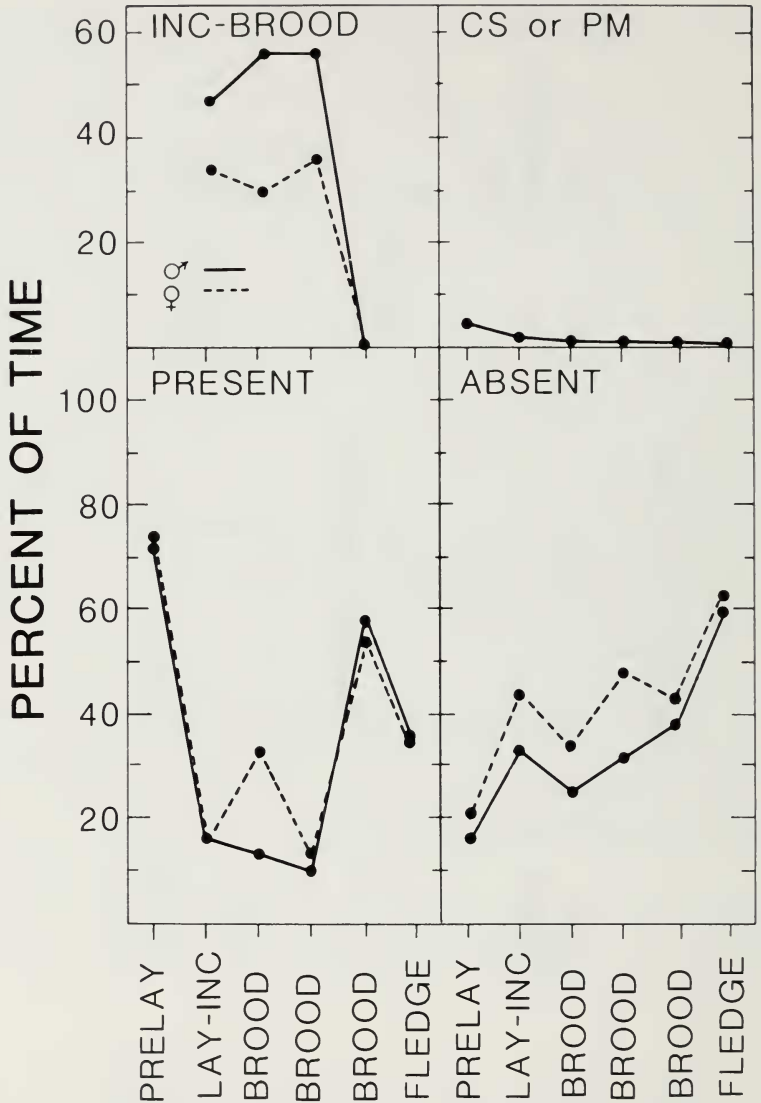


FIG. 2. Percent of time Blue-eyed Shags spent engaged in incubating or brooding, courtship or pairbond maintenance (CS or PM), present at the nest (resting, standing, preening), and absent from the nest. The breeding season is divided into prelaying, laying-incubation, three divisions of the brooding period (early, middle, and late), and the fledging period.

TABLE 2
MEAN DAILY ENERGY EXPENDITURE BY BLUE-EYED SHAGS DURING EACH STAGE OF THE BREEDING SEASON

	N ^a	Males		Females	
		kJ/d	DEE/SMR	kJ/d	DEE/SMR
Prelaying	8	2598 ± 127.6 ^b	1.80	2180–2186 ± 22.7 ^c	1.70
Laying-incubation	7	2754 ± 43.2	1.91	2384–2390 ± 34.4	1.85–1.86
Early rearing	2	2688 ± 4.3	1.86	2330 ± 75.8	1.81
Middle rearing	3	2574 ± 41.7	1.78	2571 ± 68.0	2.00
Late rearing	12	2844 ± 29.5	1.97	2443 ± 34.0	1.90
Fledging	23	2501 ± 26.3	1.73	2212 ± 8.9	1.72
Mean		2660	1.80	2353–2355	1.83

^a Number of nests observed for 24 h or from dawn to dusk.

^b Mean ± SE.

^c Range given is for minimum and maximum cost of egg production (see text).

pared with the males' increase. Data are too few in early and middle rearing for statistical comparisons, but males and females appeared to feed chicks with equal frequency. Because they were at the nest more, males spent more time in nest maintenance. Shags often preened and rested while incubating or brooding chicks, but this is not illustrated in the figures.

After the chicks grew into the late rearing stage, male and female time budgets became approximately equal as females decreased foraging time and increased nest-centered activities (Figs. 1, 2). Females still allocated more time to foraging than did males, and both sexes foraged more after chick fledging (Figs. 1, 2). Although chicks no longer required brooding during the late rearing period, one parent was always present, perhaps for protection from skuas. This resulted in an increase in presence at the nest for both sexes (Figs. 1, 2). During the fledging period, females usually spent the night on a rocky peninsula near the colony as did some males, probably to escape the vigorous and incessant begging of the chicks. Time on the rocky peninsula accounted for the majority of time represented as "present at the nest" (Figs. 1, 2).

Daily Energy Expenditure.—Daily Energy Expenditures (Table 2) differed between sexes within each period of the breeding cycle (paired *t*-test, $t = 4.84$, $df = 5$, $P < 0.005$). However, when DEE/SMR ratios were compared (i.e., when weight was accounted for), there were no significant differences even when the maximum cost of egg production was added to the females' DEE (paired *t*-test, $t = 0.244$, $df = 5$, $P > 0.5$). The DEE/

SMR ratios ranged from 1.70 to 2.00, and are, therefore, among the lower values listed by King (1974) from other avian studies.

The DEE estimates assumed a 20-km round-trip flight for both sexes each day. If, instead, the shags flew 30 km or 40 km, the DEE would be increased about 6.3% or 12.7%, respectively.

We do not believe that our observations altered the normal time budgets. In the austral summer of 1978–79, chick survivorship varied between 44 and 82% in different sections of the colony. The lowest survivorship occurred in sections of the colony that we disturbed during banding, and time budgets were not collected from these birds. Experience in handling the birds lessened disturbance in 1979–80, and undisturbed sections of the colony experienced similar reproductive success (25%) to those in which chicks were weighed and banded and adults were observed. All observed shag colonies on the Antarctic Peninsula experienced low reproductive success that summer (Maxson and Bernstein 1980).

DISCUSSION

The data indicate similarities in time and energy budgets for both sexes of Blue-eyed Shags. The similarities are due, in part, to the similar activity patterns (Bernstein and Maxson 1984), but other factors also affect the energy allocation.

It is difficult to determine how climate affected energy budgets. Berry (1976) found that climatic factors determining onset of gular flutter interacted complexly for the Cape Cormorant (*P. capensis*), and the fact that Blue-eyed Shags showed no clear patterns of gular flutter supports Berry's (1976) observations. Although ambient temperatures affect energy expenditure, Blue-eyed Shags reduced heat loss by various body postures that minimized exposure of fleshy parts and by lack of wing-spreading, possibly to conserve heat (Bernstein and Maxson 1982b). Additionally, Guard and Murrish (1975) reported that the Blue-eyed Shags' high blood viscosity might help to conserve heat, and Dunn (1979) reviewed studies documenting thermoregulatory adaptations of seabirds at high latitudes that reduce energy costs. Therefore, we feel that failure to include energy of thermoregulation will result in minimal error to estimation of DEE, and it should not affect comparisons between sexes substantially.

The high SMR directly affects the energy budget. Ricklefs and Matthew (1983) reviewed studies documenting elevated SMR in high latitude birds, but no explanation was apparent for the trend. The high SMR had several implications for Blue-eyed Shags. Twice the amount of food was necessary to support a Blue-eyed Shag compared with a similarly sized shag in lower latitudes with a lower SRM. Another important consequence was that egg formation became relatively cheap in terms of SMR (see below).

Chicks did not require direct parental attention other than feeding during late-rearing and fledging periods, and adults of both sexes spent equal time in activities (Figs. 1, 2). Montevecchi and Porter (1980) noted constant parental attendance of Northern Gannet (*Morus bassanus*) chicks for protection from antagonistic neighbors, but we did not observe neighboring adults attacking chicks.

It is not known how long parents fed chicks, but Snow (1960) observed 100-day-old chicks of the Shag (*P. aristotelis*) being fed. We observed that recently fledged chicks returned to their nests in all-juvenile groups approximately 1 h before adults. They were then fed by parents, usually in the late afternoon. Juveniles were seen foraging with small groups of adults by mid-February, and most left the colony on foraging flights by early March.

Our data on foraging behavior are similar to those of other studies. Kooyman (1975) reported dive times for this species as ranging between 5 sec and 2.5 min. There was no apparent pattern of dive and interdive times, and shags appeared incapable of a series of lengthy dives, as noted by Croxall and Prince (1980). Van Dobben (1952), Stonehouse (1967), and Siegfried et al. (1976) also observed shag species resting for long periods between foraging bouts as we described, and foraging shags were always observed near land in the Palmer Station area and during R.V. Hero cruises along the Antarctic Peninsula. It is likely that they foraged near the bottom in littoral waters. Shaw (pers. comm.) noted that during October–November 1980, Blue-eyed Shags had to fly 20–25 km each day in order to feed, and the distance traveled daily is probably locally and seasonably different.

Females need additional nutrients during synthesis of eggs (Ashmole 1971), and this may have influenced the slightly greater amount of time female shags foraged during prelaying and laying–incubation. However, given the low energy cost of eggs, this may not be a substantial factor in the energy budget of females.

Most similarities in DEE's between sexes and breeding periods can be explained by similar allocations of time to activities with the same approximate energy costs. About 90% of any day was spent either away from the colony, collectively called foraging, or in nest-related behavior such as preening, resting, standing, incubating, or brooding. All of these activities required similarly low energy output. Male energetic costs of gathering nest material usually equalled or exceeded the females' maximum daily energy costs of egg formation, and this supports the contention that, in some birds, the males' investment in prelaying activities might equal the females' investment in eggs (Gladstone 1979).

Accuracy of our DEE estimations is reduced by our lack of knowledge

of the precise time spent in flight, unknown energy costs of incubation (Walsberg 1983), and our lack of knowledge of the extent of postfledging parental care. Regarding energy for incubation, it seems logical that an incubating shag could have shunted heat to its feet within the shelter of the nest without large energy losses to the environment.

Both sexes of the Blue-eyed Shag, therefore, allocate approximately equal amounts of energy in reproduction. These proximate energy allocations are important because future reproduction and survival can be hindered if adults expend too much energy in a breeding season (Ashkenazie and Safriel 1979, Drent and Daan 1980, Montevecchi and Porter 1980). Although Mugaas and King (1981) found that DEE did not reflect equal energy expenditures between the sexes in the monogamous Black-billed Magpie (*Pica pica*), energy use does reflect equal sharing of reproductive effort in Blue-eyed Shags.

SUMMARY

Time-budget data were collected for Blue-eyed Shags (*Phalacrocorax atriceps bransfieldensis*) in Antarctica and converted to energy budgets to measure proximate energy allocation to reproduction. Time budgets were similar for both sexes, and about 90% of the 24-h activities involved low energy expenditure behavior such as preening, resting, standing, incubating, brooding, and foraging. Birds were classified as foraging when away from the colony, and although the capture of food was energetically costly, most of this time was actually spent preening, standing, or resting on shore between foraging bouts. DEE/SMR ratios were similar for both sexes, indicating equal energy investment in reproduction. Male courtship behavior equalled or exceeded female energy investment in egg production. The additional energy cost of egg production was low because of altricial eggs that were small relative to the weight of females, a 2.59-day laying interval, and the high SMR of the Blue-eyed Shags. Both sexes, therefore, shared equally in the energetics of reproduction.

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